$=0.62$ cu. mm. calculated, $=0.63$ cu. mm. found.

The rate of production of helium per year per gram of radium $=163$ cu. mm. calculated, $=164$ cu. mm. found.

B. B. BOLTWOOD

A SUGGESTED EXPLANATION OF "ORTHOGENESIS" IN PLANTS

THE purpose of this paper is not to discuss what is called orthogenesis in plants in general, but to cite certain notable illustrations of it, and to suggest a possible explanation. There may be some difference of opinion as to the proper definition of orthogenesis, but it is used in this paper as standing for progressive evolution in a given direction, in contrast with more or less successful variations in several directions, involved in the theories of natural selection and mutation.

My thesis is not to prove that orthogenesis differs in kind from such explanations of evolution as natural selection or mutation, but that the persistent variation which results in what is called orthogenesis is in response to a persistent change in the conditions of living. It is an explanation of orthogenesis which contradicts its original meaning and makes it a physical rather than a vitalistic phenomenon.

Another prefatory statement should be made. The conclusions reached in this paper are not simply inferences from a series of observations, but are based chiefly upon the results of experimental work which indicates that the changes called for can be induced as responses to changed conditions.

The gymnosperms are unique among the great plant groups in the length of their available history, recorded in such a way that our knowledge of the group may be said to be fairly continuous. Other great groups are either relatively short-lived, or their records, at least so far as our knowledge of them is concerned, are very discontinuous. As a consequence, many lines of advance among gymnosperms can be traced in unbroken series from the Devonian to the present time, involving structures that have been assumed to be beyond the influences of external conditions. I wish to call attention to four such lines of advance, and to draw certain conclusions which have some bearing upon evolutionary theory.

1. *The Egg.*—A remarkable series of progressive changes is recorded as one traces the development of the female sex organ (archegonium) from the most primitive gymnosperms to the most recent. The gradual change consists in the shifting of the time of appearance of the archegonium in the ontogeny of the gametophyte (the sexual individual). In the most primitive gymnosperms the archegonia appear at what may be called the full maturity of the gametophyte, just as they do in the prothallia of ordinary ferns. An unbroken series can be traced, representing an earlier and earlier appearance of archegonia in the ontogeny of the gametophyte, extending from full maturity to very early embryonic stages. In this ontogeny three stages may be roughly distinguished: (1) free nuclear division; (2) primary wall formation; (3) growth of tissue. It is toward the end of the third stage that archegonia appear in the most primitive gymnosperms; and the gymnosperms of to-day, whose archegonia are late in appearing, as the Cycads, are primitive in this feature, though they may be advanced in some others.

As one proceeds with the history of the group, it can be observed that the appearance of archegonia shifts back through the third stage, more and more tissue being developed after their appearance. Next they are observed forming at the second stage, that of primary wall formation. In

Torreya, for example, as soon as there are walled cells at all, the archegonium initials become recognizable; and all of the tissue development (the so-called endosperm) appears after the archegonia are under way.

Finally the shift is made into the first stage of gametophyte development, that of free nuclear division, so that, of course, there is no archegonium initial, and no archegonium, as in *Gnetum,* the egg being organized in connection with a free nucleus. If one were to continue this progress into Angiosperms, he would find eggs appearing earlier and earlier in the free nuclear stage of the gametophyte, so that the free nuclei are relatively few when eggs are organized; and recently a form has been found in which the megaspore nucleus organizes an egg directly, so that this backward movement in ontogeny has reached its limit, at least in one extreme case.

Such a series of progressive changes in gymnosperms, and there are several others equally distinct, furnishes us perhaps our most impressive illustration of what Naegeli called "progressive evolution," which we have come to call orthogenesis. Here is a steady progress in a given direction through an immeasurable lapse of time, during which, presumably, the plants have been exposed to every conceivable change of conditions.

Recent experimental work upon sexuality in plants, however, may suggest an explanation for this phenomenon among gymnosperms. It is now known that the appearance of gametes (the sexual cells) is in response to certain conditions affecting metabolism. When the gamete is associated with a sex organ, as the archegonium, the conditions for gamete formation are the conditions for archegonium formation. In other words, the essential response is the gamete; a sex organ may or may not be involved. Speaking in very general terms, the conditions that favor gamete formation are associated with minimum vegetative activity. These conditions may affect the plant as a whole, in such forms as algæ, or only certain protoplasts, and in them the sex response occurs. It follows in the case of our gymnosperms that any change of conditions shortening the period of vegetative activity, would thereby hasten the appearance of eggs in the ontogeny of the gametophyte. This is exactly the result that would follow the differentiation of the year into definite seasons. In other words, this progressive change in the time of the appearance of the eggs of gymnosperms seems to hold some relation to the evolution of climate. It is significant, perhaps, that the two great living groups of gymnosperms, Cycads and Conifers, are contrasted not only in the feature under discussion, but also in geographic distribution. The Cycads, primitive in the late appearance of eggs, are tropical; while the Conifers, advanced in the early appearance of eggs, are found in the sharply differentiated seasons of the temperate regions. In any event, we know that a gamete is a response to conditions affecting unfavorably the ordinary metabolism of a plant; and the most regularly recurring variable that affects natural vegetation is climate.

2. *The Proembryo.*—A parallel illustration of progressive evolution is presented by the proembryo of gymnosperms. Unfortunately the embryos of paleozoic gymnosperms have not as yet been found, not because they did not exist, as some have imagined, but because we have not been sectioning the proper seeds. In any event, it is now becoming safe to predict their general character.

In the most primitive gymnosperms the proembryo is an extensive tissue, completely filling the large egg, best illustrated by *Gingko* among living forms. Just as in the case of nuclear division in any large cell, there is a certain amount of free nuclear division before wall formation begins. In these primitive gymnosperms successive free nuclear divisions continue until numerous free nuclei are distributed throughout the egg, and then primary wall formation fills the egg with proembryonic tissue, consisting sometimes of hundreds of cells. The progressive change consists in the earlier and earlier appearance of wall formation in the history of the embryo, thus restricting free nuclear division, and limiting the extent of proembryonic tissue.

In the Cycads, for example, permanent proembryonic tissue occurs in every amount, from almost filling the egg (not completely filling it, as in *Gingko*) to a relatively small amount at one pole of the egg, as in *Zamia*. When this type of change is followed into the Conifers, the proembryonic tissue is found to be reduced to a few cells, and in some of the Gnetales there is no free nuclear division, so that the proembryo, in the ordinary sense, has disappeared, a condition which characterizes the angiosperms. The conditions that favor wall formation and inhibit continued free nuclear division are, of course, unknown in a definite way, but that this phenomenon is a response to some progressive change in conditions is evident.

After recognizing the kind of changes that influence gamete formation, and that perhaps explain the progressive evolution of the archegonium situation, it is of interest to discover whether these two series of progressive changes in general proceed *pari passu*. Without going into details, it may be said in general that they do. In other words, forms whose archegonia appear toward the maturity of the gametophyte have large proembryos; while those forms that have eliminated archegonia have also eliminated proembryos (that is, in the gymnosperm sense of free nuclear division as a preliminary stage). Whether declining metabolic activity favors wall formation, as contrasted with free nuclear division, as it certainly does gamete formation, I am not prepared to say; but the situation lends itself to experimental answer.

These two illustrations of progressive evolution suggest that orthogenesis does not differ from other kinds of evolution in being some kind of determinate mechanism that does not respond to a changing environment, but only in that it is a response to some progressive evolution of environment. Of course, we all realize that the word environment covers a tremendous complex of interacting factors, which the ecologist is trying to disentangle. The point made here, however, is not to suggest the factors that have been instrumental in bringing these changes to pass, but to suggest that the factors, whatever they may be, are external, and that the changes are responses. If the change is progressive, the variation in conditions is progressive.

3. *The Cotyledons.*—No feature of the embryo of gymnosperms has been more discussed than their mixture of dicotyledony and polycotyledony. The discussion has revolved about the conviction that one of these conditions must be primitive and the other derived from it. To some, dicotyledony is the primitive condition, because Cycads and Bennettitales are dicotyledonous, and they seem most primitive in other features. According to this view polycotyledony has been derived from dicotyledony by splitting. To others, polycotyledony is the primitive condition, chiefly because it is characteristic of Abietineæ, and in that case dicotyledony has been derived from it by fusion.

It would be a boon to one or the other of these schools if the embryos of Cycadofilicales or Cordaitales should be discovered, and found to be positively either polycotyledonous or dicotyledonous. My prophecy is that they will be found to be both. A study of cotyledony in general has shown that these two conditions, and also monocotyledony, are merely different, and often variable final expressions of a common method of development. A cotyledonary zone or ring always develops around the growing point, and upon this ring a variable number of primordia appear, nearly always more than finally develop. The whole ring continues to develop in connection with one or two or more growing points, the others having been checked by conditions easily explained by the ontogeny of the embryo, especially by the time and position of the appearance of the immediately succeeding members. When one finds not only dicotyledony, but also polycotyledony, among the Monocotyledons, it becomes apparent that the number of cotyledons is a variable. The wonder is that it is as constant as it appears to be.

The interesting evolutionary feature is that polycotyledony is so much more common among gymnosperms than among angiosperms. It is perhaps safe to say that it was as common among most primitive gymnosperms as was dicotyledony; or rather that the number of cotyledons was much more variable than in any living group of seed plants. This interesting situation is still further emphasized by the remarkable constancy of dicotyledony in the Dicotyledons and of monocotyledony in the Monocotyledons, but I know of none of them in which less than four cotyledonary growing points start. The conditions that seem to determine the number of cotyledons to be developed by a cotyledonary ring are too numerous to be discussed here, but in general they have to do with the rate of growth of the subsequent members of the embryo. For example, if the subsequent leaves begin to appear almost immediately and develop vigorously, the cotyledonary ring usually becomes one-sided in development, and the result is a single large cotyledon in an apparently terminal position. Many monocotyledonous embryos, in which for some reason there is an elongation of the stem before the first leaves begin a vigorous growth, develop two cotyledons, as in the case of numerous grasses. This is the usual sequence in Dicotyledons; while in polycotyledonous forms there is much delay in the appearance of the subsequent members, and no inhibition of cotyledon primordia. All this variation in the number of cotyledons suggests variations in the conditions of growth, since it depends upon rate of growth in the so-called "plumule."

4. *The Seed.*—Another noteworthy illustration of progressive evolution in gymnosperms, associated with the same conditions that seem to have determined the changes previously cited, is the progressive simplification of the ovule and seed. As yet the most primitive ovule is not available, and the hiatus in our knowledge between the fern sporangium or sorus, and the most primitive known ovule is complete. In that unknown region heterospory developed, and then the seed-forming ovule, but the steps are left to conjecture. The interesting fact, however, is that the most primitive ovules and seeds we know are the most complex, and that there has been a progressive simplification through the whole series of seed plants. This simplification has not only involved the layers of the testa, as often pointed out; but its gradual progress is most completely shown by the vascular supply to the ovule and seed. The very gradual elimination of the vascular elements is a measure of the progressive simplification of the whole structure. We have found that the vascular supply does not determine the structure; but the structure determines the vascular

supply. Ovule and seed formation are associated with the closing activities of a period of growth, and any shortening of this period by a sharp differentiation of seasons should leave some impress upon ovule and seed development. This progressive simplification of the ovule deserves attention in the effort to discover its conditions; and the whole story, excepting the introductory chapter, is recorded in the history of gymnosperms.

In conclusion it may be emphasized that the gymnosperms, with their unparalleled perspective, are not only of importance in connection with the problems of the origin of seed plants and of angiosperms, but also in developing some conception of evolutionary progress quite apart from fluctuating variations or even mutations, and certainly beyond the control of any experimental work in genetics. It is obvious now that the phenomenon of progressive evolution in plants is not to be explained by any so-called "inherent tendency," but rather as a continuous response to progressive changes in the conditions for vegetative activity. When these conditions are analyzed, the response called orthogenesis in plants will become to some extent an index of the evolution of climate.

JOHN M. COULTER
UNIVERSITY OF CHICAGO

THE CONVOCATION WEEK MEETINGS OF SCIENTIFIC SOCIETIES

THE American Association for the Advancement of Science and the national scientific societies named below will meet at Columbus, Ohio, during convocation week, beginning on Monday, December 27, 1915:

American Association for the Advancement of Science.—President Dr. W. W. Campbell, Director Lick Observatory; retiring president, Dr. Charles W. Eliot, Harvard University; permanent secretary, Dr. L. O. Howard, Smithsonian Institution, Washington, D. C.; general secretary, Mr. Henry Skinner, Academy of Natural Sciences, Logan Square, Philadelphia, Pa.; secretary of the council, Professor W. E. Henderson, Ohio State University.

Section A—Mathematics and Astronomy.—Vice-president, Professor A. O. Leuschner, University of California; secretary, Professor Forest R. Moulton, University of Chicago, Chicago, Ill.

Section B—Physics.—Vice-president, Professor Frederick Slate, University of California; secretary, Dr. W. J. Humphreys, U. S. Weather Bureau, Washington, D. C.

Section C—Chemistry.—Vice-president, Professor W. McPherson, Ohio State University; secretary, Dr. John Johnston, Geophysical Laboratory, Washington, D. C.

Section D—Mechanical Science and Engineering.—Vice-president, Bion J. Arnold, Chicago; secretary, Professor Arthur H. Blanchard, Columbia University, New York City.

Section E—Geology and Geography.—Vice-president, Professor C. S. Prosser, Ohio State University; secretary, Professor George F. Kay, University of Iowa.

Section F—Zoology.—Vice-president, Professor V. L. Kellogg, Stanford University; secretary, Professor Herbert V. Neal, Tufts College, Mass.

Section G—Botany.—Vice-president, Professor W. A. Setchell, University of California; secretary, Professor W. J. V. Osterhout, Harvard University, Cambridge, Mass.

Section H—Anthropology and Psychology.—Vice-president, Professor G. M. Stratton, University of California; secretary, Professor George Grant MacCurdy, Yale University; New Haven, Conn.

Section I—Social and Economic Science.—Vice-president, Geo. F. Kunz, New York; secretary, Seymour C. Loomis, 69 Church St., New Haven, Conn.

Section K—Physiology and Experimental Medicine.—Vice-president, Professor F. P. Gay, University of California; secretary, Professor C.-E. A. Winslow, Yale University.

Section L—Education.—Vice-president, Professor E. P. Cubberley, Stanford University; secretary, Dr. Stuart A. Courtis, Detroit, Mich.

Section M—Agriculture.—Vice-president, Professor Eugene Davenport, University of Illinois; secretary, Dr. E. W. Allen, U. S. Department of Agriculture, Washington, D. C.